

A STUDY OF *PADINA ANTILLARUM* (KÜTZING) PICCONE AND A COMPARISON WITH *P. TETRASTROMATICA* HAUCK (DICTYOTALES, PHAEOPHYTA)

Michael J. WYNNE

Department of Biology and Herbarium, University of Michigan
Ann Arbor, Michigan 48109, U.S.A.
Fax: 734-647-0884; e-mail address: mwynne@umich.edu

ABSTRACT — Holotype material of *Zonaria antillarum* Kützing [= *Padina antillarum* (Kützing) Piccone] was located in MEL and examined. The provenance of this poorly known taxon is Trinidad in the West Indies. A comparison of this alga is made with other species of *Padina*, and the conclusion is made that it is a taxonomic synonym of *P. tetrastromatica* Hauck. The priority of *Zonaria antillarum* Kützing (1859) over *P. tetrastromatica* Hauck (1887) necessitates the replacement of the latter name with *P. antillarum* (Kützing) Piccone. A listing of currently recognized species of *Padina* is provided.

RÉSUMÉ — L'holotype de *Zonaria antillarum* Kützing [= *Padina antillarum* (Kützing) Piccone] a été localisé à MEL et examiné. Ce taxon mal connu provient de Trinidad, aux Antilles. Cette algue a été comparée aux autres espèces de *Padina* et a été mise en synonymie avec *P. tetrastromatica* Hauck. La priorité de *Zonaria antillarum* Kützing (1859) sur *P. tetrastromatica* Hauck (1887) implique de remplacer le second par *P. antillarum* (Kützing) Piccone. Une liste des espèces de *Padina* actuellement reconnues est aussi fournie dans cet article. (Traduit par la Rédaction)

KEY WORDS: marine algae, *Padina*, *P. antillarum*, *P. tetrastromatica*, Phaeophyta, *Zonaria antillarum*.

INTRODUCTION

Zonaria antillarum Kützing (1859) has remained a poorly known taxon of brown algae of unspecified provenance and uncertain status. Although the specific epithet refers to the Antilles of the tropical western Atlantic, the species was not included in the floristic treatment of this region by Taylor (1960) nor picked up by Wynne (1986) in his catalogue of algae for this same domain. Its inclusion, as *Padina antillarum* (Kützing) Piccone (1886), in the recent catalogue of Indian Ocean marine algae by Silva *et al.* (1996) came to my attention as well as fact that its type locality had not been specified by Kützing (1859). The basis for the Indian Ocean record was Piccone's (1886, 1889) report of its presence from Singapore as well as his transfer of this species from *Zonaria* to *Padina*. The

discovery of the Holotype collection of this alga in the National Herbarium of Victoria (MEL), Melbourne, allowed for its examination and a clarification of its status.

In Vol. 9 of his *Tabulae phycologicae* Kützing (1859) described a number of new species of Dictyotales from various locations around the world, including some from the western Atlantic (Table 1), on the basis of specimens in the Sonder Herbarium. Following the death of Sonder, Ferdinand Mueller, founder of the National Herbarium of Victoria, purchased the Sonder Herbarium from Sonder's nephew (Ducker, 1981a, 1981b), which explains how many of Sonder's types came to reside in MEL.

Table 1. Taxa of Dictyotales newly described from the western Atlantic by Kützing (1859).

Taxon	Provenance	Currently accepted name
<i>Dicyota antiguae</i>	Antigua, Lesser Antilles	<i>D. guineensis</i> (Kützing) <i>P. crouan</i> & H. Crouan
<i>D. cervicornis</i>	Key West, Florida	<i>D. cervicornis</i>
<i>D. ciliolata</i>	La Guaira, Venezuela	<i>D. ciliolata</i>
<i>D. cuspidata</i>	Veracruz, Mexico	<i>D. cuspidata</i>
<i>D. indica</i>	Havana, Cuba	<i>D. cervicornis</i>
<i>D. pardalis</i>	« E mari Antillarum » [« Senegambia » on type sheet]	<i>D. cervicornis</i>
<i>D. pinnatifida</i>	Antigua, Lesser Antilles	<i>D. pinnatifida</i>
<i>Dictyota subdentata</i>	Antilles Lesser Antilles	<i>D. mertensii</i> (Martius) Kützing
<i>Spatoglossum versicolor</i>	Brazil	<i>Stylopodium zonale</i> (Lamouroux) Papenfuss
<i>Zonaria gymnospora</i>	St. Thomas, U. S. Virgin Islands	<i>Padina gymnospora</i> (Kützing) Sonder
<i>Zonaria antillarum</i>	Provenance not cited	<i>Padina antillarum</i> (Kützing) Piccone

Zonaria antillarum has remained of uncertain status. J. Agardh (1882) regarded *Z. antillarum* along with Kützing's *Z. gymnospora* and his concept of *Z. variegata* as taxonomic synonyms of *Padina durvillaei* Bory de Saint-Vincent. Piccone (1886, 1889) transferred the species to *Padina* while recording it from Singapore; he made no reference to J. Agardh's (1882) treatment. De Toni (1895) and Weber-van Bosse (1913) made passing reference to *Z. antillarum*, simply accepting J. Agardh's interpretation. Børgesen (1914) stated that J. Agardh was wrong in referring *P. antillarum* to *P. durvillaei* but did not indicate how he would treat it. Neither Murray (1888-1889) nor Taylor (1960) made reference to *Zonaria* (or *Padina*) *antillarum* for the Caribbean. In her unpublished dissertation Thivy (1945) discussed the species on the basis of Kützing's original description and figures and stated that *Zonaria antillarum* probably applied to a *Zonaria* and not to a *Padina*. Her reason for this idea was that the sori of Kützing's plant were described as consisting of clusters of sporangia with hairs arising among the sporangia as in *Zonaria*. Yet Thivy recognized that in *Zonaria* an indusium covers the sori, whereas an indusium was not figured for Kützing's plant. The sporangial sori of *Zonaria* often bear sporangia intermixed with multicellular paraphyses (Allender & Kraft, 1983), but this feature is not characteristic of all species in the genus (Womersley, 1987; Phillips, 1997). Teo & Wee (1983) reported three species of *Padina* from Singapore: *P. gymnospora* (Kütz.) Sond. (erroneously as a species with distromatic thalli, and thus probably *P. boergesenii* Allender & Kraft), *P. boryana* Thivy (as *P. tenuis*), and *P. tetrastromatica* Hauck, but they made no reference to Piccone's (1886) earlier record of *P. antillarum* from there.

MATERIALS AND METHODS

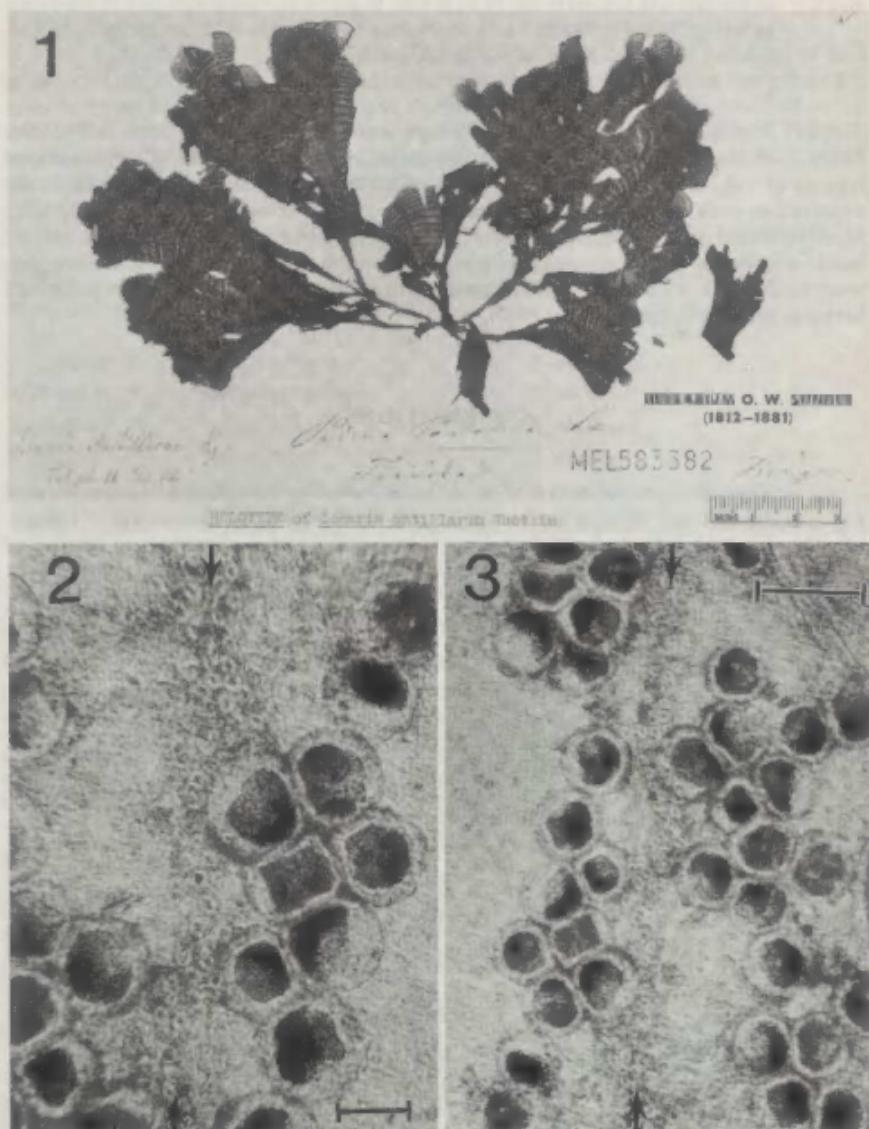
The holotype of *Zonaria antillarum* was received on loan from MEL (No. 583382). Small portions of the specimen, including distal, mid-blade, and proximal regions of the blade were rehydrated, gently cut away and mounted on glass slides for observation with a standard Zeiss research microscope. Some portions of blade were hand-sectioned using a single-edged razor blade. Line-drawings were made with a camera lucida attached to the microscope, and photomicrographs, using Kodak T-MAX 100 film, were made with a camera-back attached to the same microscope. Abbreviations of herbaria follow Holmgren *et al.* (1990).

OBSERVATIONS

The holotype specimen of *Zonaria antillarum* (Fig. 1) is labeled "Padina Pavonia Lx", "Trinidad", and "Krüger" in Sonder's hand and "Zonaria Antillarum Kg." "Tab. ph. IX, Tab. 72." in Kützing's hand. Mrs Doris Sinkora, former algal curator at MEL, has added (dated 19.iii.1981) to the herbarium sheet the information that the collector "Hermann Krüger (1818-1864) was born in Hamburg, went to live in Trinidad in 1841 and changed the spelling of his name to Crüger, was Colonial Botanist & Superintendent of the Botanic Garden there [from] 1857 till his death in 1864". This information was derived from Urban (1902).

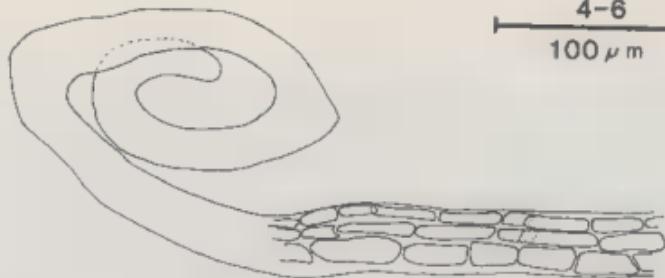
Kützing (1859, Tab. 72, fig. II) depicted the habit of the plant as deeply divided into cuneate to flabellate segments; a cross-section of the lower part of the thallus, which is four cell-layers in thickness, with hair-forming articulated filaments, which constitute the stipe; a mid-thallus cross-section, three cell-layers in thickness, with sporangia and short secondary filaments interspersed among the sporangia; and a surface view of the thallus showing sporangia and secondary filaments, the latter viewed from the top.

The holotype specimen consists of a number of flabellate segments reaching 9 cm in length and deeply divided to the base. The narrow basal parts are densely covered with rhizoids. Individual segments are 2.0-3.0 cm broad. There is no obvious calcification. The circinnately inrolled margin (Fig. 4) confirms the fact that it is a *Padina*, not a *Zonaria* as Thivy (1945) suggested. Sagittal sections of the thallus in the distal region show that it is three cell layers in thickness (Fig. 5), whereas sections of the thallus in mid-blade show four cell layers (Fig. 6). Almost all segments are fertile, bearing bands of sori on only the inferior surface of the blade, *i.e.*, the surface of the blade opposite the side toward which the margin is curled. Soral bands appear close to the growing margin, and they are regularly spaced at a distance of 1.0-1.6 mm. The prominence and thickness of the soral regions give the blades a distinctly corrugated aspect. The division of some of the reproductive organs indicates that they are tetrasporangia rather than oogonia. Mature sporangia are 70-90 µm in diameter. There is no indication of an indusium over mature sori. The sporangia closely abut a continuous line of hairs (a piliferous zone) (Figs 2, 3, & 7). Typically, all that remains of the hairs are the basal cell remnants. Paraphyses of the type that occurs in *Zonaria* were not present. The short multicellular filaments shown by

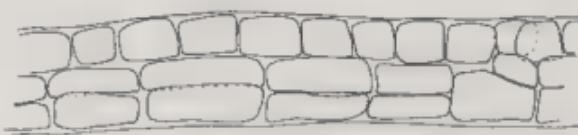


Figs 1-3. *Padina antillarum* (based on holotype of *Zonaria antillarum* in MEL). Fig. 1. Habit. Figs 2 & 3. Surface view of soral regions, showing sporangia lying on both sides of zone of hairs (arrows). Scale bars in Figs 2 & 3 = 50 µm.

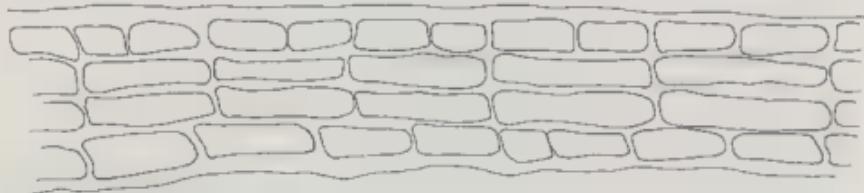
4

4-6
100 μm

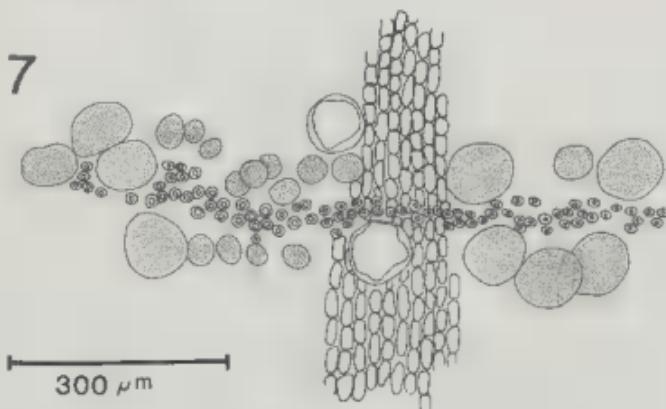
5



6



7



300 μm

Figs 4-7. *Padina antillarum* (based on holotype of *Zonaria antillarum*). Fig. 4. Sagittal section of apical region of blade showing circinnately involuted margin. Fig. 5. Sagittal section of distal region of thallus. Fig. 6. Sagittal section of mid region of thallus. Fig. 7. Schematic surface view of soral region, showing arrangement of sporangia on either side of zone of hairs.

Kützing (1859, pl. 72, fig. II, c) are merely hairs. The sporangia are densely arranged along both sides of this zone of hairs (Figs 2 & 3), at times giving the impression of being intermixed with the hairs, as Kützing (1859) depicted them.

The characteristics seen in the holotype of *Zonaria antillarum* present a persuasive case that it is the same as *Padina tetrastromatica* Hauck. According to Jaasund (1976) *P. tetrastromatica* is easily recognized because of the double lines of sporangia on either side of a line of colorless hairs and because it is the only East African species of *Padina* that occurs on open shores with surf activity, which explains the tendency of the thallus to split into narrow segments. Other hallmark features of *P. tetrastromatica* are that thalli are rarely encrusted with limestone, that tetrasporangial sori are non-indusiate, and that thalli are primarily four cell layers in thickness. All of these characteristics are shared by *P. antillarum* and *P. tetrastromatica*, pointing to their taxonomic identity. Evidence for the conspecificity of these two taxa will be presented in the Discussion, especially in reference to the observations made on *P. tetrastromatica* by Gaillard (1967).

Lawson & John (1987) described thalli of West African *Padina tetrastromatica* to be often distinctly corrugated, to be repeatedly divided into delicate and narrow segments, uncalcified, with the zones of hairs 1-1.5 mm apart; thallus four cells thick throughout; sori developing close to and on either side of each hair zone, without an indusium. This description closely matches the above account of the holotype of *Zonaria antillarum*.

DISCUSSION

In Taylor's (1960) comprehensive flora of the eastern tropical and subtropical coasts of the Americas, six species of the brown algal genus *Padina* were recognized. Two of these species (*P. haitiensis* and *P. perinduslata*) were newly described and credited to Francesca Thivy, whose doctoral dissertation had been completed at the University of Michigan in 1945. She was also credited with the new combination *Padina pavonica* (Linnaeus) Thivy to replace the incorrect name *P. pavonia* (Linnaeus) Lamouroux. Another Caribbean species was *P. vickersiae* Hoyt in Howe (1920), which had been the alga depicted as *Zonaria variegata* (Lamouroux) C. Agardh by Kützing (1859, pl. 73) and as *Padina variegata* (Lamouroux) Hauck by Vickers (1908, pl. VIII) and by Børgesen (1914, figs 157-161). Børgesen (1920) had applied *P. howeana* nov. nom. to this same entity.

In the ensuing years following Taylor's (1960) treatment the list of species of *Padina* has been altered. Gaillard (1975) suggested that *P. haitiensis* was conspecific with *P. sanctae-crucis* Børgesen, but due to the scarcity of specimens she refrained from making a formal proposal to merge the two taxa. So *P. haitiensis* continues to be recognized. Taylor's (1960) observation that *Dictyterpa jamaicensis* Collins (1901) was "a growth stage of a *Padina*, perhaps of various species, but certainly of [*P. sanctae-crucis*]" caused Papenfuss (1977) to propose *P. jamaicensis* (Collins) Papenfuss as the correct name. But because of the uncertainty which species the type of *D. jamaicensis* corresponded to, Silva *et al.* (1987) preferred to retain the name *P. sanctae-crucis*. Earle (1969) described *P. profunda* as a new species from the Gulf of Mexico. Although *P. boryana* Thivy in Taylor and *P. caulescens* Thivy in Taylor were included in Wynne's (1986) checklist, no basis could later be found for their inclusion, and they have been deleted from the checklist revision (Wynne, 1998).

In his floristic account of the marine algae of Trinidad, Richardson (1975) listed only two species of *Padina*: *P. vickersiae* and *P. gymnospora*. Allender & Kraft (1983) clarified previous taxonomic confusion concerning these two names. Most authors (Børgeesen, 1914; Taylor, 1960; Earle, 1969) had misinterpreted *P. gymnospora* to be a tristromatic species, even though Børgeesen (1914) appreciated the fact that this interpretation was in conflict with one of the figures given in Kützing's (1859) plate 71. Allender & Kraft's (1983) examination of the type (*Zonaria gymnospora* Kützing) in MEL showed it to be four cell layers in mid frond and six-eight cell layers near the base, which was in agreement with Kützing's protologue. Thus, Allender & Kraft (1983) concluded that *P. vickersiae* must be treated as a taxonomic synonym of *P. gymnospora* and that a new species, *P. boergesenii* Allender & Kraft, was to be recognized for the tristromatic species which had been mistakenly identified as *P. gymnospora*.

Womersley (1987) reported *Padina gymnospora* (in the sense of Allender & Kraft, 1983) from southern Australia and characterized it as four cells thick above and 6-8(-9) cells thick in mid and lower parts. According to Womersley an indusium over the sporangia is "absent or slight". In their account of this species from the southeastern coast of the United States, Schneider & Searles (1991) described the plants as becoming deeply laciniate, with cuneate-spatulate to fan-shaped segments. They said that the reproductive structures occurred in one or two bands midway between hairlines on both surfaces but primarily on the ventral surface. The oogonia were protected by a thin, evanescent covering of sterile cells, and the tetrasporangia also had sterile coverings.

Differences of opinion exist on the thallus thickness of *P. tetrastromatica*. In Hauck's (1887) original account of the species the thalli were described as three layers of cells near the apex and four (rarely six) layers toward the base. According to Thivy (1945, p. 184) *P. tetrastromatica* cannot be considered as having more than four layers of cells in the frond. When six or seven layers are present, they are found only in the "Flachtriebe" (= ligulate branch) of the germling which may persist at the base of the stipe of the adult plant. The "Flachtriebe" is distinguishable from the frond proper. Weber-van Bosse (1915) said that her plants from the East Indies were four cell layers thick from close to the apex down to the base. Børgeesen (1936) reported on material from Ceylon to have four cell layers, while in material from India Børgeesen (1930) observed 2 cell layers near the growing edge and three or four cell layers in the basal regions. Allender & Kraft (1983) referred to *P. tetrastromatica* as a "basically tristromatic species" which tended to become four layers thick near the base.

The most detailed description of *P. tetrastromatica* was provided by Gaillard (1967), who based her account on herbarium material including three syntype specimens (in L) and recent collections from Dakar, Senegal, West Africa. The specimen collected by Hildebrandt (Hauck 68) from Meith, Somalia, and depicted by Gaillard (1967, fig. 1) was designated the "Typus" according to P. Audiffred (pers. comm.). Gaillard found that the type specimens all presented a tetrastromatic structure. Gaillard observed that the specimens from West Africa were four layers of cells in their broadest part; only at the base could there be six cell layers.

Gaillard (1967) found that an indusium present in the early stages of tetrasporangial sorus formation was soon shed. All authors are in agreement that mature tetrasporangial sori lack an indusium. Gaillard observed the rows of reproductive organs to be almost contiguous to the hairs and that it is impossible to measure the distance between sporangia and hairs. Gaillard also confirmed Hauck's (1887) observation that some plants in this species can produce plantules, which arise in the same position as the tetrasporangial sori. Lawson & John (1977) also noted this same phenomenon in plants of this species from the Cap Blanc Peninsula of West Africa.

Although Allender & Kraft (1983) depict *Padina tetrastromatica* as bearing sporangia on only one surface of the thallus, Gaillard (1967) and Schnetter (1976) depict sporangia in this species as being sometimes produced on both blade surfaces. Gaillard described the sporangia to be arranged in sori abutting the hair zones on the inferior side, whereas on the superior blade surface the sporangia are borne at mid-distance between the soral bands on the opposite face, although they are most often poorly developed and the sporangia are intermixed with hairs instead of surrounding the hair bands. Gaillard observed this arrangement both in the syntype specimens and in those from Senegal. She also stated that in the majority of specimens of *P. tetrastromatica* from elsewhere, the reproductive organs are localized only on the inferior face and form only very sporadic groups on the other face. In MICH holdings of *P. tetrastromatica* the production of sporangia on both blade surfaces, as Gaillard (1967) depicted them, was observed in two West African collections (leg. D. M. John 6430C from Ghana; leg. G. W. Lawson A1186 from the Gold Coast), but in numerous Philippine specimens sporangia were produced only on the inferior face. So this is regarded as a variation within the species.

No world monograph of *Padina* has been published in a modern context, but a survey of the literature has shown that 32 species are currently recognized. Data on these are summarized in Appendix 1. How many true biological species these represent remains to be determined.

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Appendix 1. Currently Recognized Species of *Padina*

1) *P. antillarum* (Kützing) Piccone, 1886, p. 36.

Basionym: *Zonaria antillarum* Kützing, 1859, p. 29, pl. 72, fig. II.

Type locality: not indicated. Holotype in MEL: Trinidad, Lesser Antilles, West Indies.

Tax. syn.: *P. tetrastromatica* Hauck, 1887, p. 43.

Type locality: Meith, Somalia. Lectotype in L (Hauck No. 68 = Gaillard, 1967, fig. 1).

Distribution: widely distributed in Indian Ocean, including East Africa, Yemen, Oman, Arabian Gulf, India, Pakistan, Ceylon; Philippines, Malaysia, Indonesia, northeastern Australia, China, West Africa, Colombia, Venezuela. According to Thivy (1945), the report of *P. tetrastromatica* by Setchell & Gardner (1930) from Pacific Mexico is most likely *P. crispata*.

References (all of the following were as *P. tetrastromatica*): Weber-van Bosse, 1913, pp. 180-181; Børgesen, 1930, p. 172, fig. 10, pl. II; Durairatnam, 1961, p. 36, pl. VII, figs 4, 5, pl. XXVI, fig. I; Gaillard, 1967, p. 447-463; Srinivasan, 1969, p. 26, pl. XXVI; Schnetter, 1976, p. 76, pl. IX, fig. I, K; Pl. XI, fig. B; Jaasund, 1976, p. 45, fig. 90; Price *et al.*, 1978; Ngan & Price, 1979, p. 8, 1980, p. 186; Lawson & John, 1987, p. 131, pl. 15, figs 4 & 5; Tseng, 1983, p. 200, pl. 101, fig. 2; Allender & Kraft, 1983, p. 89, fig. 7F; Jones, 1986, p. 31, pl. 6; Ganeshan, 1990; Shameel & Tanaka, 1992; Ormond & Banaimoon, 1994; Wynne & Luong-Van Thinh, 1997, p. 85; Wynne & Jupp, 1998, p. 11.

2) *P. arborescens* Holmes, 1896, p. 251, pl. 12, fig. 1.

Type locality: Enoshima, Japan. Holotype in BM.

Distribution: Japan, Korea, Fujian and Guangdong provinces of China, Hong Kong, Taiwan, and the Philippines.

References: Okamura, 1929, p. 3, pl. 251, fig. 10, pl. 252; Yamada, 1931, p. 67; Lee, 1964, p. 53, pl. 7, fig. 2; Chihara, 1970, p. 24, pl. 12(1); Tseng, 1983, p. 196, pl. 99, fig. 4; Lewis & Norris, 1987, p. 12; Silva *et al.*, 1987, p. 77; Kajimura, 1996, p. 10, figs 1-16.

3) *P. australis* Hauck, 1887, p. 44.

Type locality: Cape York, northern Australia (earlier treated as *P. gymnospora* by Sonder, 1871). Holotype in L.

Distribution: Japan, Philippines, Hong Kong, Taiwan, Thailand, Indonesia, Malaysia, Papua New Guinea, Lord Howe Island, eastern and northern Australia, New Zealand ("?"), and West Africa.

References: Yamada, 1931, p. 70, text-fig. 2 and pl. XVIII; Okamura, 1932, p. 88, pl. 295, figs 1-4; Lee, 1964, p. 53, pl. 6, fig. 6, and pl. 7, fig. 1; Egerod, 1974, p. 151, fig. 85; Magruder & Hunt, 1979, p. 47; Trono & Ganzon-Fortes, 1980, p. 41, fig. (s. n.); Allender & Kraft, p. 85, figs 5 C, 6 B; Tseng, 1983, p. 198, pl. 100, fig. 1; Lewis & Norris, 1987, p. 12; Lawson & John, 1987, p. 128, pl. 15, fig. 9; Farrant & King, 1989, p. 388, fig. 12; Adams, 1994, p. 89; Coppejans *et al.*, 1995, p. 184, fig. 22; Calumpang & Menéz, 1997, p. 126.

var. *cuneata* Tanaka & Nozawa, 1962, p. 179, pl. I, A, fig. 1.

Type locality: Amadomari, Nishino-omote, Tanegashima, Japan. Holotype presumably in KAG.

4) *P. boergesenii* Allender & Kraft, 1983, p. 87, figs 6 C, H & I, 7 C & D)

Type locality: Danish West Indies [= U. S. Virgin Islands]. Holotype in MEL.

Distribution: broadly distributed in tropics. According to Allender & Kraft (1983) voucher material needs to be examined to determine whether various records of *P. gymnospora* [e.g., Thivy (1959) from India and Taylor (1966) from the Philippines] refer to *P. boergesenii*.

References: Vickers, 1908, p. 37, pl. VII (as *P. gymnospora*); Børgesen, 1914, p. 202, figs 155, 156 (as *P. gymnospora*); Taylor, 1960, p. 237 (as *P. gymnospora*); Sartoni, 1975, p. 289, figs 9 & 11 (as *P. gymnospora*); Schnetter, 1976, p. 73, pl. IX, fig. H; pl. XI, fig. A (as *P. gymnospora*); De Clerck & Coppejans, 1996, p. 230, figs 48, 50-51; González-González *et al.*, 1996, p. 94.

5) *P. boryana* Thivy in Taylor, 1966, p. 355, fig. 2.

Type locality: "Friendly Islands" = Tonga, Polynesia. Holotype in NY.

Distribution: tropical Indian and Pacific Oceans, West Africa.

Misapplied name: *Padina commersonii* Bory de Saint-Vincent (1828). See Silva *et al.* (1996, p. 603), who explain that *P. commersonii*, a name that had been traditionally applied to the present taxon, is an illegitimate substitute for *P. tenuis* (C. Agardh) Bory de Saint-Vincent (1827). The basionym of this latter name, *Zonaria pavonia* var. *tenuis* C. Agardh (1824) was demonstrated by Womersley & Bailey (1970) to be the same as *Lobophora variegata* (Lamouroux) Womersley ex Oliveira.

References: Okamura, 1932, p. 89, pl. 295, figs 5-11 (as *P. commersonii*); Tsuda, 1972, p. 98, pl. 5, fig. 4 (as *P. tenuis*); Levring, 1943, p. 176, fig. 1 B-F; Tanaka & Nozawa, 1962, p. 180, pl. II, A, fig. 2 (as *P. commersonii*); Egerod, 1974, p. 150, fig. 84 (as *P. tenuis*); Kapraun & Bowden, 1978, p. 200 (as *P. tenuis*); Allender & Kraft, 1983, p. 83, figs 5 D & E, 6 A (as *P. tenuis*); Tseng, 1983, p. 198, pl. 100, fig. 2; Lawson & John, 1987, p. 130; Farrant & King, 1989, p. 390, fig. 15 (as *P. tenuis*); Tsuda, 1991, p. 45; Coppejans *et al.*, 1995, p. 188.; N'Yeurt, 1996, p. 402, fig. 108f (as *P. tenuis*).

6) *P. caudescens* Thivy in Taylor, 1945, p. 99.

Type locality: off Isla Maria Magdalena, Las Tres Marias, Nayarit, México. Holotype in LAM.

Distribution: Pacific Mexico and Gulf of California.

References: Dawson, 1959, p. 18; Chavez, 1980, p. 48; Mendoza-Gonzalez & Mateo-Cid, 1986, p. 421; González-González *et al.*, 1996, p. 155.

7) *P. concrescens* Thivy in Taylor, 1945, p. 102.

Type locality: Black Beach Anchorage, Isla Santa María, Galapagos Islands. Holotype in LAM.

Distribution: Galapagos Islands, Pacific Mexico.

Reference: González-González *et al.*, 1996, p. 155.

8) *P. crassa* Yamada, 1931, p. 67, pl. XVII, fig. 2.

Syntype localities: Sagami Prov., Iyo Prov., Nagato Prov., Chikuzen Prov., Hizen Prov., Mutsu Prov., Izumo Prov. Holotype presumably in SAP.

Distribution: China, Japan, Korea, Hong Kong, eastern Australia including Lord Howe Island.

References: Okamura, 1932, p. 87, pl. 294, figs 5-11; Lee, 1964, p. 53, pl. 6, fig. 3; Chihera, 1970, p. 24, pl. 12 (2); Allender & Kraft, 1983, p. 87, figs 6 G, 7 A & B; Tseng, 1983, p. 198, pl. 100, fig. 3; Farrant & King, 1989, p. 388, fig. 13; Tsuda, 1991, p. 45; Kajimura, 1993, p. 19, figs 1-17.

9) *P. crispata* Thivy in Taylor, 1945, p. 100.

Type locality: Golfo Dulce, Costa Rica (Pacific coast). Holotype in LAM.

Distribution: Pacific Central America, Pacific Mexico, Pacific Colombia

References: Chavez, 1980, p. 47; Schnetter & Bula Meyer, 1982, p. 64, pl. 10, fig. H; Mateo-Cid & Mendoza-González, 1991a, p. 24; González-González *et al.*, 1996, p. 156.

10) *P. distromatica* Hauck, 1887, p. 43.

Type locality: Meith, Somalia (a Hildebrandt collection). Holotype in L.

Distribution: East Africa, Seychelles, Indonesia, Philippines.

References: Sartoni, 1975, p. 289, fig. 10.

11) *P. dubia* Hauck, 1887, p. 45.

Type locality: Meith, Somalia. Holotype in L.

Distribution: East Africa, Pakistan, India.

References: Sacco, 1965, p. 550, pl. XXXIII; Panikkar & Chauhan, 1991a, p. 139, figs 1-35, & 1991b, p. 149, 1-22.

12) *P. durvillaei* Bory de Saint-Vincent, 1829, p. 147, Atlas, 1826, pl. 21, fig. 1.

Type locality: Concepcion, Chile. Syntype material in PC.

Distribution: Pacific Mexico, Gulf of California, Mexico; Pacific Panama and Costa Rica; Pacific Colombia; Galapagos Islands; tropical West Africa.

References: Taylor, 1945, p. 101; Schnetter & Bula Meyer, 1982, p. 65, pl. X, fig. 1; Lawson & John, 1987, p. 130, pl. 15, figs 6, 7; Gonzalez-Gonzalez et al., 1996, p. 156.

forma *obscura* Piccone, 1886, p. 36.

Type locality: Rio de Janeiro, Brazil. Holotype presumably in VER.

13) *P. elegans* Koh ex Womersley, 1987, p. 220, figs 74B, C, 75K-M.

Type locality: Muldrup Reef, Cottesloe, Western Australia. Holotype in UWA.

Distribution: Port Denison, Western Australia, to Pearson Island, South Australia.

14) *P. fernandeziana* Skottsberg ■ Levring in Levring, 1941.

Syntype localities: numerous stations listed in the Juan Fernandez Islands, Chile. Holotype in GB.

Distribution: as above.

References: Etcheverry, 1986, p. 95, pl. III.

15) *P. fraseri* (Greville) Greville, 1830, p. xliv.

Basionym: *Zonaria fraseri* Greville, 1829, p. 423 & 424, pl. XXVI.

Type locality: New Holland = Australia [New South Wales or Victoria according to Womersley, 1987, p. 218]. Holotype in E. fide Womersley (1987).

Tax. syn.: *P. tristromatica* Levring, 1942, p. 60, figs 1 & 2; syntype localities: San Felix and San Ambroiso, Juan Fernandez Islands, Chile (fide Gaillard, 1968). Syntypes in GB.

Distribution: coast of Australia from Warrnambool, Victoria, around south-eastern Australia to the mid north coast of New South Wales, and the north coast of Tasmania; Norfolk Island; San Ambroiso and San Felix, Juan Fernandez Islands, Chile.

According to Womersley (1987) the record by Lindauer et al. (1961) of *Padina fraseri* from the Kermadec Islands of New Zealand is more likely *P. gymnospora*, and the report by Taylor (1966) from the Philippines is likely to be of a different species. Adams (1994) also reported *P. fraseri* from the Kermadecs, but the plants were small and sterile.

References: Womersley, 1967, p. 222; Gaillard, 1968; Allender & Kraft, 1983, p. 88, fig. 6 D; Womersley, 1987, p. 217, pl. 2, fig. 1; figs 73D, 75D-G; Farrant & King, 1989, p. 390, fig. 14; Adams, 1994, p. 89, pl. 25.

16) *P. glabra* Gaillard, 1966, p. 222, figs 1-3.

Type locality: Dakar, Senegal, West Africa. Holotype presumably in PC but not located.

Distribution: West Africa and India.

References: Silva et al. (1996).

17) *P. gymnospora* (Kützing) Sonder, 1871, p. 47.

Basionym: *Zonaria gymnospora* Kütz., 1859, p. 29, pl. 71, fig. II.

Type locality: St. Thomas, U.S. Virgin Islands, Caribbean. Holotype in MEL (Allender & Kraft, 1983).

Distribution: Caribbean, Caribbean Mexico, West Africa, Hawaii, western Australia.

Tax. syn.: *P. variegata* sensu Børgesen, 1914, p. 205; *P. vickersiae* Hoyt in Howe, 1920, p. 595 (type locality: Fort Macon jetty, Beaufort, North Carolina, USA) (fide Allender & Kraft, 1983); *P. howeana* Børgesen, 1920, p. 442.

References: Vickers, 1908, p. 37, pl. VIII (as *P. variegata*); Børgesen, 1914, p. 205, figs 157-161 (as *P. variegata*); Hoyt, 1920, p. 456, fig. 22; pl. XCII, figs 1 & 2; pl. CXIV, figs 1-3; Taylor, 1960, p. 236, pl. 34, fig. 1 (as *P. vickersiae*); Earle, 1969, p. 172, fig. 61 (as *P. vickersiae*); Schnetterer, 1976, p. 77, pl. IX, fig. G; pl. XII, fig. A (as *P. vickersiae*); Allender & Kraft, 1983, p. 87, fig. 7E; Lawson & John, 1987, p. 131, pl. 16, fig. 5 (as *P. vickersiae*); Wormsley, 1987, p. 217, figs 73C, 75A-C; Littler *et al.*, 1989, p. 112; Mateo-Cid & Mendoza-González, 1991, p. 78; Littler & Littler, 1997, p. 79, fig. 100.

18) *P. haitiensis* Thivy in Taylor, 1960, p. 632 (& 235), pl. 75, fig. 1.

Type locality: Isla Tortuga, Hispaniola. Holotype in MICH.

Distribution: Hispaniola and Turks Islands, Caribbean, Caribbean coast of Mexico and Colombia.

References: Schnetterer, 1976, p. 74, pl. X, fig. B; Mateo-Cid & Mendoza-González, 1991b, p. 78; González-González *et al.*, 1996, p. 94.

19) *P. japonica* Yamada, 1931, p. 69, pl. XIX, fig. 2.

Syntype localities: Mikawa Prov., Iyo Prov., Nagato Prov., Higo Prov., Satsuma Prov., Echigo Prov., Japan. Holotype presumably in SAP.

Distribution: Japan, Taiwan, Caroline Islands.

Gaillard (1975) offered evidence to treat this taxon as conspecific with *P. sanctae-crucis*, but subsequent workers have continued to recognize it.

References: Okamura, 1932, p. 87, pl. 294, figs 1-4; Tanaka & Nozawa, 1962, p. 182, fig. 3; Trono, 1969, p. 36; Magruder & Hunt, 1979, p. 49; Lewis & Norris, 1987, p. 12; Kajimura, 1994, p. 72.

20) *P. jonesii* Tsuda, 1972, p. 98, pl. 5, fig. 3.

Type locality: Dougle Reef, Guam. Holotype in US.

Distribution: Guam; Xisha Islands (Guangdong Province, China).

References: Tseng, 1983, p. 198, pl. 100, fig. 4.

21) *P. melemele* Abbott, 1996, p. 143, figs 1-3.

Type locality: Illo Point, Moloka'i Island, Hawaii. Holotype in BISH.

Distribution: also known from O'ahu Island, Hawaii.

22) *P. mexicana* Dawson, 1944, p. 231, pl. 52, fig. 2.

Type locality: Turner's Island reef, off Tiburon Island, Gulf of California, Mexico. Holotype in LAM.

Distribution: Pacific Mexico, tropical West Africa.

Reference: Lawson & John, 1987, p. 131, pl. 15, figs 8a-c; Mateo-Cid & Mendoza-González, 1991a, p. 24; González-González *et al.*, 1996, p. 156.

23) *P. minor* Yamada, 1925, p. 251, fig. V.

Type locality: Garanbi, Taiwan. Holotype presumably in SAP.

Distribution: Taiwan, Guam, Fiji, Japan, China, the Philippines, Papua New Guinea, Arabian Gulf.

References: Okamura, 1932, p. 56, pl. 279, figs 6-9; Chihara, 1970, p. 24, pl. 12(3); Tsuda, 1972, p. 97, pl. 5, fig. 2; Kapraun & Bowden, 1978, p. 200; Trono & Ganzon-Fortes, 1980; Tseng, 1983, p. 200, pl. 101, fig. 1; Verheij & Prud'homme van Reine, 1993, p. 429, fig. 5d, pl. 10: 7; Coppejans *et al.*, 1995, p. 184; De Clerck & Coppejans, 1996, p. 230, figs 49, 52; Calumpang & Meñez, 1997, p. 126.

24) *P. pavonica* (Linnaeus) Thivy in Taylor, 1960, p. 234.

Basionym: *Fucus pavonicus* Linnaeus, 1753, p. 1162.

Type locality: "In Mari Europae australis". Holotype presumably in LINN.

Thivy's binomial replaced the incorrect name *P. pavonia* (Linnaeus) Lamouroux (1816), which was based on *Fucus pavonius* Linnaeus, 1759, p. 1345.

Distribution: England, Atlantic coast of France and Spain, Mediterranean, Azores, Canary Islands, Bermuda and Caribbean; widely distributed in Indian Ocean

Tax. syn.: *P. mediterranea* Bory de Saint-Vincent, 1827, p. 590; *P. oceanica* Bory de Saint-Vincent, 1827, p. 590 (*fide* I. Agardh, 1848).

References: Harvey, 1846-1851, pl. XCI; Reinke, 1878, p. 15, pl. 2, figs 18-22, pl. 3, pl. 4, figs 1-12; Hamel, 1939, p. 343, fig. 57, 1-II; Price *et al.*, 1979, p. 1-67; Schnetter & Bula Meyer, 1982, p. 66, pl. X, fig. K-M; Coppejans, 1983, pl. 55; Cabioch *et al.*, 1992, p. 165, fig. 178; Littler & Littler, 1997, p. 81, fig. 102; González-González *et al.*, 1996, p. 94.

25) *P. perindusiasi* Thivy in Taylor, 1960, p. 632 (& 235), pl. 75, fig. 2.

Type locality: Southwest Channel, Dry Tortugas, Florida. Holotype in MICH.

Distribution: Dry Tortugas, Florida, Gulf of Mexico.

References: González-González *et al.*, 1996, p. 94.

26) *P. plumbea* (Areschoug) Levring, 1940, p. 226-227, fig. 5.

Basionym: *Zonaria plumbea* Areschoug, 1851, p. 25-26; *Chlidophora plumbea* (Areschoug) Papenfuss, 1940, p. 204, fig. 5.

Type locality: Port Natal [= Durban], South Africa. Holotype presumably in S.

Distribution: South Africa.

27) *P. profunda* Earle, 1969, p. 167, figs 62-68.

Type locality: a site "in 60 m depth about 19 mi. offshore from Loggerhead Key, Dry Tortugas, Florida". Holotype in FH.

Distribution: Dry Tortugas, Florida, Gulf of Mexico, North Carolina.

References: Schneider & Searles, 1973, p. 202; 1991, p. 162, fig. 195.

28) *P. ryukyuana* Y. P. Lee & Kamura, 1991, p. 92, figs 1-13.

Type locality: Bisezaki, Okinawa, Ryukyu, Japan.

Distribution: Okinawa, Japan. Holotype in CNU.

29) *P. sanctae-crucis* Børgeesen, 1914, p. 201, figs 153 & 154.

Type locality: St. Croix, U. S. Virgin Islands. Holotype in C.

Distribution: Caribbean, Gulf of Mexico, Pakistan, Bangladesh, Papua New Guinea, Australia.

References: Taylor, 1960, p. 237, pl. 34, fig. 2; Chapman, 1963, p. 23, fig. 18 (as *Dictyerpa jamaicensis*); Earle, 1969, p. 171, fig. 59; Gaillard, 1975, p. 85, figs 1-4; Schnetter, 1976, p. 75, pl. X, fig. A; Womersley, 1987, p. 219, figs 74A, 75H-J; Littler *et al.*, 1989, p. 114; Coppejans *et al.*, 1995, p. 184, fig. 23; Littler & Littler, 1997, p. 81, figs 101 (as *P. jamaicensis*) and 103; González-González *et al.*, 1996, p. 94.

Tax. syn.: *P. jamaicensis* (Collins) Papenfuss, 1977, p. 272.

Basionym: *Dictyerpa jamaicensis* Collins, 1901, p. 251.

Type locality: Manchioneal, Jamaica. Syntypes: *Phycotheca-Boreali Americana* 780; lectotype apparently not yet designated.

30) *P. somalensis* Hauck, 1887, p. 45.

Syntype localities: Scaria and Lasgori, Somalia.

Distribution: Somalia. Holotype in L.

31) *P. stipitata* T. Tanaka & Nozawa in Tanaka, 1960, p. 100, text-figs 8-10, pl. V, A, B.

Syntype localities: Funauke, Iriomote Island, Ryukyu Islands; Koniya, Amami Islands, Japan. Syntype specimens presumably in KAG; lectotype not yet designated.

Distribution: Ryukyu Islands and Amami Islands, southern Japan.

References: Tsuda, 1991, p. 45.

- 32) *P. thivyaee* Doty & Newhouse, 1966, p. 139, as "*P. thiryi*" figs 1, 2 a & b.

Type locality: reef flat seaward of the Natatorium, Waikiki, Oahu, Hawaii.
Holotype in BISH.

Distribution: Hawaiian Islands.

References: Magruder & Hunt, 1979, p. 49.